Totem: The University of Western Ontario Journal of Anthropology

Volume 22 | Issue 1 Article 3

2014

Mating Behavior in Australopithecus and Early Homo: A Review of The Diagnostic Potential of Dental Dimorphism.

Joseph J. Werner
University of Alberta, jwerner@ualberta.ca

Mating Behavior in Australopithecus and Early Homo: A Review of The Diagnostic Potential of Dental Dimorphism.

Abstract
Dental dimorphism is one of the primary means by which the mating systems of extinct hominins are studied. Its use has been particularly significant for describing the behaviors of *Australopithecus* and early *Homo*, and consequently the factors involved in the evolution of our own species. Analysis however, has tended to produce ambiguous and contrasting results, with no firm agreement as to what mating strategies these genera practiced. Interpretation is confounded by numerous problems such as a generally poor understanding of how dental dimorphism develops in primates, and what factors influence its expression. It is also not well known how these factors interact with different aspects of the dentition and to what relative extent these aspects are diagnostic of mating behavior. The failure in many cases to firmly establish the sex of fossil specimens has likewise hampered the interpretations of sexual dimorphism and by extension, mating behavior. Lastly, the ability to correlate dental dimorphism with mating systems, even in living primates, has met with only moderate success. For these reasons it is argued that dental dimorphism be used only to support the most general assertions about hominin social behavior.

Acknowledgements
The submitted paper benefited greatly from the input of Dr. Lesley Harrington, whose comments and assistance were invaluable.

Mating Behavior in *Australopithecus* and Early *Homo*: A Review of the Diagnostic Potential of Dental Dimorphism

J. Jeffrey Werner

Introduction

During the Pliocene and Lower Pleistocene (5.2 – 1.5 million years ago), the ancestors of modern humans experienced a significant change in body size and proportions, which is believed to have resulted in a more human-like pattern of sexual dimorphism[1] (Anton and Snodgrass 2012; McHenry and Coffing 2000; Spoor *et al.* 2007). These changes are consistent with reduced male intrasexual competition and are thought to signal a change in mating behaviour from a form of polygyny to monogamy (Strier 2007). Understanding how sexual dimorphism was related to mating systems and social behaviour in these species is therefore crucial for determining how and why the contemporary human pattern of sexual dimorphism evolved.

In addition to body size, sexual differences are also commonly expressed in the teeth of dimorphic animals, such as primates, and are one of the most powerful means of identifying the group composition and mating systems of paleo-species (Gordon, Green, and Richmond 2008; Hillson 1996; Kay *et al.* 1988; Strier 2007; Wolpoff 1976; Wood, Li, and Willoughby 1991). The dimorphic nature of primate dentition is especially important for the study of basal hominin genera such as *Australopithecus* and early *Homo*, for which teeth are preferentially preserved due to the resilient properties of tooth enamel relative to bone (Conroy 2005). The interpretation of the dental evidence for these genera however is still highly varied and a number of dramatically different mating strategies have been proposed, including: single-male/multi-female, multi-male/multi-female, and monogamous systems. While using dentally dimorphic traits such as canine height as a proxy for mating behaviour is common in palaeontology, it is nevertheless problematic for a number of reasons. Firstly, the influence of alternate sources of dental dimorphism such as diet, intra-female competition, correlated response, and predator defense are not well understood and rarely accounted for in predictions of mating behaviour. This makes detecting and isolating morphological differences caused by sexual selection from these alternate sources of variation difficult if not impossible. Secondly, unrelated dimorphic attributes, such as canine-size and body-size, are the result of dissimilar selective process and may consequently represent different aspects of the social and environmental context. Furthermore, the relative diagnostic value of each of these measures has yet to be fully determined, which makes comparisons with living, analogous species difficult. Thirdly, disagreement over species classification, and low sample sizes also prevent a secure sex estimation of individual specimens, confounding current understandings of sexual dimorphism in *Australopithecus* and early *Homo*. Lastly, even in living primate species, mating systems correlate only modestly well with observed sexual dimorphism, which is only further complicated paleontologically by the three previous factors.

For the reasons listed above, it will be argued that the dimorphic dentitions of early hominin taxa are not always strong indicators of intrasexual conflict intensity or mating behaviour by themselves and that they must be used in association with other dimorphic characters.

[1] Sexual dimorphism refers to the differences in size, morphology, colouration, and behaviour of males and females of the same species. (Strier 2007)

Background: Sociobiology and Sexual Dimorphism

In primate species, sexual dimorphism develops primarily as a result of sexual selection, which exerts unalike pressures on males and females, as each sex competes in its own fashion to reproduce successfully (Strier 2007). This type of competition is more studied in males where it has been shown to contribute most substantially to size dimorphism (Plavcan 2012b). Contests between males for access to mates are frequently typified by physical force, displays of dominance, and elaborate performances. If, in one of these arenas, a heritable trait increases male reproductive success, selection favours it. As a result, in many primate species, males are larger than females and support a more elaborate array of weaponry and ornaments (Wilson 1975).

The effects of intrasexual conflict tend to produce similar patterns of morphological adaptation which are visible at a taxonomic scale and can be systematized in semi-predictable ways. Primatologists typically recognize two to three primary types of mating systems, each partly identifiable by the degree of sexual dimorphism, and intrasexual conflict intensity that is exhibited (Harvey, Kavanagh, and Clutton-Brock 1978; Plavcan 2001; Strier 2007).

A common classification scheme is laid out by Strier (2007), who recognizes three divisions. Firstly, single-male/multi-female groups are characterized by a dominant male who presides over a particular community, often debarring other males from the group entirely. With only one male permitted to mate, competition is highest in this group structure, and single-male/multi-female groups produce the most extreme examples of sexual dimorphism. Secondly, multi-male/multi-female groups are composed of an equal member-ratio of both sexes, and generally practice a form of polygyny. The intensity of competition between males differs between multi-male/multi-female species, resulting in highly variable levels of sexual dimorphism between taxa. In primate social groups that practice monogamous pair-bonding, or polyandry, males and females are of comparable size and morphology, taking equivalent roles in the defence of their territory and the care of their offspring. Monogamous and polyandrous primates are rare compared to those that practice other mating strategies.

Dental Variation as a Result of Sexual Selection

Male and female body-size coefficients are one of the most recognizable examples of sexual dimorphism, but sex dependent disparities in tooth-size and morphology also form the basis of predictions regarding the social organization and mating behaviour of primate species (Plavcan 2001). For example, some scholars have suggested that the size of the posterior teeth (pre-molars and molars) in non-human primates is a viable indicator of body-size and thus body-size dimorphism (Hillson 1996; Wolpoff 1976). Despite the effects of diet (metabolic scaling factors) on crown dimensions, the size of the molars, and to a lesser extent the pre-molars, appear to scale allometrically to the size of the organism. That is, the posterior teeth remain roughly proportional to the rest of the animal as body-size changes (Gingerich 1977; Gingerich, Smith, and Rosenberg 1982; Hillson 1996; Wood 1979). Although research on other animal species, such as birds, has revealed significant differences in the size and shape of feeding structures between males and females who occupy different dietary niches, primates subsist on similar foods irrespective of sex and thus do not exhibit divergent dietary adaptations

(Plavcan 2001). Simply then, a larger primate species would be expected to have larger molar teeth than a smaller one; and similarly, males of a greater size would be anticipated to possess larger molars than females of a smaller size. This relationship is thought to allow the relative tooth sizes of the posterior dentition in non-human primates to serve as a rough proxy from which to infer body-size differences and thus conflict intensity (Wolpoff 1976). Like other tooth classes however, the size and morphology of the posterior dentition responds to factors other than conflict intensity; such as diet. What is more, pre-molars and molars are less representative of dimorphic distance (when scaled for size) relative to other types of teeth (Hillson 1996).

As the posterior dentition tends to be monomorphic, unless an extreme difference in male and female body-size exists, the relatively dimorphic buccolingual diameter[2] and height of the canines is thought to make them a better indicator of inter-male conflict intensity (Hillson 1996). Enlarged canine teeth are hypothesized to be particularly important for males as they double as weapons in direct physical competition with other males, or as a means of communicating dominance (Harvey, Kavanagh, and Clutton-Brock 1978; Hillson 1986; Sperber 2013; Strier 2007**)**.

Despite inherent difficulties, many researchers argue that since not all primates are uniformly dimorphic, differences in the size of their canine and posterior teeth should allow paleoanthropologists to make assumptions about the relative intensity of intrasexual competition in extinct species, and relate it to other forms of social behaviour and group structure (Hillson 1996; Strier 2007; Wilson 1975; Wolpoff 1976; Wood, Li, and Willoughby 1991).

Dental Dimorphism in Plio-Pleistocene Hominins (5.2-1.5 mya)

The earliest identified members of the *Homo* genus (*Homo habilis / Homo rudolfensis*) were in place in East Africa by at least the beginning of the Pleistocene around 2.6 million years ago (mya) (Bobe and Behrensmeyer 2004; Wood 1996). While this group is often distinguished by an expansion in brain volume, their post-cranial morphology remained very similar to their likely precursors, the australopithecines, who evolved in South and East Africa during the Pliocene (5.3-2.6 mya). Both *Australopithecus* and early *Homo* shared a mixture of primitive and derived features which suggest a mixed adaptation to terrestrial bipedalism as well as arboreal life (Stringer and Andrews 2005). Many scholars also propose that the range of sexual dimorphism exhibited by these species was large, easily matching and possibly exceeding the maximum dimorphism observed in surviving primates such as gorillas and orangutans (Gordon, Green, and Richmond 2008; Grine *et al.* 2012; Hausler and Schmid 1995, 1997; Lockwood *et al*. 1996; Plavcan 2001, 2012; Tague and Lovejoy 1998; Wolpoff 1976). It follows from what is known about sexual dimorphism in extant primates that fierce male intrasexual competition typified these two genera and likely revolved around a form of polygynous group structure.

High levels of dimorphism in *Australopithecus* and *Homo* is supported in part by measurements of their dentition. When plotted in aggregate, the posterior tooth-size of these hominins shows a bi-modal pattern, likely indicating a significant difference in the body-mass between sexes (Wolpoff 1976). What is contradictory is that while the posterior dentitions of these

[2] The diameter of the tooth measured from the side closest to the tongue to the side closest to the lips.

taxa were highly dimorphic, the differences in their canine-sizes were much less pronounced than those of living apes, though still somewhat in excess of human averages – a pattern that is unique in primatology (Lee 2005). What is perplexing about this template is that exaggerated body-mass dimorphism, predicted by a disparity in cheek teeth size and post-cranial remains, is associated most often with high levels of competition, while recessed canines are assumed to be evidence of low levels of intrasexual competition. This pattern has yet to be satisfactorily explained, but based on numerous analyses *Australopithecus* and early *Homo* are thought to have practiced a range of mating strategies, from single-male/multi-female mating at one extreme, to monogamy at the other (Plavcan 2012b; Reno et al. 2010). The high variance of these interpretations is symptomatic of a number of key complications. Namely, that there are numerous alternate sources of variation capable of impacting the development of sexual dimorphism which are not often well accounted for. These factors also influence different aspects of the dentition unequally, resulting in mixed or contradictory signals. Furthermore, doubt over the sex of individual fossil specimens destabilizes the already questionable correlations between dimorphic dentition and mating systems. Lastly, even in living primates where direct comparisons are possible, dental dimorphism shows only weak to moderate concomitance with mating behaviour. The following sections describe these issues in more detail as they pertain to the mating systems of the hominin genera *Australopithecus* and *Homo*. It will be advised that researchers avoid directly correlating patterns of dental dimorphism in extinct species with mating systems without consideration for these additional sources of variation.

Alternate Sources of Dental Variation

In order to reliably predict mating strategy on the basis of sex dependant morphology, a firm understanding of sexual dimorphism and its causes needs to be established. One of the primary challenges of identifying sexual dimorphism in hominin taxa is distinguishing sex dependent morphology from variation derived from other sources. These additional sources are often poorly understood, and while male-male competition is theorized to account for ~48% of the dimorphic morphology of primates, the remaining variation is not well explained (Plavcan 2012b).

Until recently it was frequently assumed, for instance, that sexual dimorphism was the result of a transformation to male morphology away from an expected ecological optimum (represented by female morphology). More recently, however, researchers have begun to evaluate the contributions of female morphology to sexual dimorphism (Plavcan 2004). In particular, female canine-size has been demonstrated to alter in response to the intensity of resource competition with other females. Unlike males, for whom the primary source of conflict is for access to mates, females compete most intensely for food. Consequently, in habitats where persistent or seasonal circumstances contribute to scarce or patchy food resources, competition between females is more intense, and female canine-size is exaggerated (Plavcan 2012b).

Additional social factors have also been shown to affect the size of primate canines. Plavcan and colleagues (1995) provided evidence that canine-size dimorphism is reduced in primate social groups in which males typically form alliances to determine the outcome of conflict. In such cases, it is hypothesized that the combative fitness of any one male is

less important than the total fighting strength of the group and his ability to form alliances. Sex dependent roles and behaviour may also exaggerate the dimorphic differences of the dentition (Leutenegger and Kelly 1977). As males in most primate social groups tend to be larger, with over-sized canines as a result of sexual selection, they are also better suited to defend against, and discourage attacks from predators. Because canines are effective weapons against both predators and antagonistic males of the same species, they are twice as likely to be selected for in males whose role it is to protect the group (Shine 1989). Such behaviours are, of course, invisible paleontologically, and the effects of alliance making and predator defense on canine size are likely to go unrecognized.

Particular characteristics of genetic inheritance may also contribute to the expression of sexual dimorphism. Autosomal genes are those that are common to both sexes and, like other genes, may become selected for under favourable environmental and social conditions. When characters determined by autosomal genes become selected for in one sex, because they are shared, an associated change in the opposite sex occurs - an effect called correlated response (Lande 1980). This is hypothesized to mitigate, to some degree, the effects of sexual selection on dimorphic attributes. For example, if selection favoured large male canines as a result of intrasexual competition, this same trait would likewise be inherited by any female offspring until the genes became decoupled as a result of additional genetic mechanisms. Problematically, it is not clear as to how and to what extent this phenomenon impacts the differences between sexes (Plavcan 2012b). The precise effects of another evolutionary process called phylogenetic inertia on sexual dimorphism are similarly unknown (Wilson 1975). Phylogenetic inertia is a mechanism for morphological stasis: if a heritable trait becomes selectively neutral, that is, it is not favoured or deleterious; it will tend to persist in a species unchanged. This phenomenon may result in a selectively neutral, dimorphic characteristic becoming preserved despite a change in behaviour.

Given that both male and female dentitions are sensitive to social and environmental conditions; it is difficult to know to what extent any particular manifestation of sexual dimorphism is the result of intrasexual competition as part of a specific mating system. As these alternate factors are as likely as not to go undetected in a fossil context, sexual dimorphism can only be partially accounted for, making an accurate determination of mating system with current models challenging.

Problems Interpreting Mixed Dimorphic Indicators

Because many elements of the hominin post-cranial skeleton and dentition are dimorphic, their relative ability to indicate aspects of social behaviour, such as mating strategy, remains to be fully determined. Moreover, as the selective pressures which act on particular dimorphic elements of the skeleton are unalike, the respective morphology of these elements is almost certainly reflective of different conditions and causes (Plavcan 2012b). The diversity of potential causes has made comparing and interpreting the dimorphic dentitions of *Australopithecus* and early *Homo* difficult because of the mixed and ambiguous behavioural signals that have emerged. A key example of this is the posterior dentitions of these genera which predict extensive body-size dimorphism, intrasexual male conflict, and likely a mating system akin to the polygyny observed in many living primates. This interpretation is contradicted by the height and breadth of the canine teeth which are relatively monomorphic, suggesting low

conflict levels. This pattern is not explainable by sexual selection alone, which cannot easily account for these divergent signs. It is clear that the canine teeth and the posterior dentition are aligned with different processes and therefore do not represent evidence of the same selective pressures. While it has not yet been determined precisely what was responsible for forcing this pattern, it is likely that factors supplementary to mating behaviour and mate competition, resulted in the dimorphic character of these species.

For Wolpoff (1976) and others (McHenry 1992, 1994a; Toth and Schick 2009; contra: Lovejoy 2009; Plavcan 2001, 2012), the apparently conflicting evidence can best be explained by the emergence of material culture during the Pliocene, leading to the diminished role of canine teeth as they were supplanted by extrasomatic means. Not only were cultural items argued to be more effective in cases of physical conflict, but that by brandishing them, early hominins could intimidate their rivals in a manner functionally equivalent to canine teeth (Gruter 1982; Wolpoff 1976). Because of the assumed simplicity of these early artefacts, a large body-size remained an important factor in the use of early tools and weapons, and consequently large, robust males continued to be selected for whereas their enlarged canines did not. While the tool-use theory is plausible, little direct evidence of this hypothesis, such as skeletal trauma has been recorded, and what does exist cannot be linked to male/male violence, let alone the use of artificial weapons (Berger 2012; Susman 2008). Others have also pointed out that the beginning of the archaeological record and the process of canine reduction in our ancestors was non-contemporaneous by at least a million years (Plavcan 2001).

Alternatively, Reno *et al.* (2003, 2005, 2010) criticize previous studies of drawing comparisons between fossil materials from significantly different spatial and temporal contexts. The improper scale of analysis, they argue, has resulted in normal temporal and spatial variation being mistakenly identified as sex differences. To correct for these problems, their work has focused on the hominin remains from AL 333 (Hadar, Ethiopia), a death assemblage dated to 3.2 mya. The remains at this site are argued to be a demographically representative sample of *A. afarensis*, including both males and females of varying ages. What Reno and colleagues (2003) observed are low levels of body-size dimorphism, in agreement with the low degree of canine dimorphism already witnessed in this group. In opposition to existing notions, their findings support a more human-like level of sexual dimorphism in *A. afarensis*. Moreover, Reno *et al.* (2003) make the assertion that the minimal sexual dimorphism revealed both dentally and skeletally at AL 333 is indicative of a monogamous mating strategy.

The continuing disagreement over the classification of *Australopithecus* and early *Homo* is largely symptomatic of the problematic nature of collectively interpreting individual indicators of dimorphism without consideration for their independent causes. This practice has the paradoxical effect of reducing certainty about past behaviours as more lines of evidence are compounded (Plavcan 2012). Despite being recognized early by authors such Leutenegger and Kelly (1977) in their study of primates, little theoretical or methodological headway has been made towards resolving the issue. More recently, Plavcan (2000; see also: Lee 2005; Plavcan and van Schaik 1997a) likewise finds in his review of the sexual dimorphism of living and extinct primates, that the occlusal-size

dimorphism of the canines is much less demonstrable of dimorphic distance than canine height or breadth. Here, even within the same tooth class, different methods of measuring dimorphism produced varying results. In order to more accurately assess dimorphic differences, and their correlates such as mating systems, a better understanding of key individuators, and how they interact to produce sexual dimorphism, is required.

Determining the Sex and Ancestry of Fossil Hominins

A necessary prerequisite to effectively evaluating sexual dimorphism is the ability to reliably differentiate male and female anatomy. While the sex of individual specimens ought to be known at the outset of analysis, it is not always the case, and the sexes of many fossils are highly provisional. The difficulty stems principally from a lack of fossil remains, which makes evaluating intrinsic population variation and sex differences nearly impossible.

In modern humans, analysis of the pelvis is the most accurate method of diagnosing sex. Because the morphology of the female pelvis must balance the conflicting requirements of locomotion and parturition, marked differences relative to the male pelvis are apparent to analysts who have demonstrated a high degree of success differentiating them. Post-cranial elements are, however, quite rare in the Plio-Pleistocene, and few pelves have been recovered from which more definitive sex determinations might be attempted. Even when pelves are recovered (*A. afarensis* and *A. africanus*), current methods of sex assessment are not yet reliable enough to confirm the sex of these specimens (Häusler and Schmid 1995). The pelvic morphology of *Australopithecus* is simply not well understood, and what is known, seems to suggest divergence from both ape and human anatomy, making the use of sex estimation models derived from either of these taxa prone to error. Moreover, many fossils, such as ST 14 (*A. africanus*) show significant evidence of plastic deformation, further complicating the picture (Berge and Goularas 2010).

As determining the sex of australopithecine pelvic remains has proven to be inconsistent, alternate techniques have been employed with varying degrees of success, most of which focus on post-cranial size metrics and dento-cranial features (Hager 1990; Tague and Lovejoy 1998). Since dimorphism in early hominins is predicted to be substantial, body-size and robusticity are commonly employed predictors of sex. Conversely, significant post-cranial differences may reflect interspecific rather than sexual variation, and the reliability of this strategy is questionable given that many of the specimens under study have not yet been classified, without contention, at the level of species (Häusler and Schmid 1995, 1997; Miller 2000; Tague and Lovejoy 1998; Wood and Quiney 1996), or even genera in some cases (Susman 2008). The dimorphic dentition of hominin conspecifics is likewise used as a sex indicator. This practice is problematic for the same reasons that body-size dimorphism is; namely, it is still unclear as to how these specimens should be assigned taxonomically, and it is very possible that the sex differences identified presently may in fact be examples of interspecific ones, if not some other form of variation.

Given the insecurity of sex estimates in australopithecines and early representatives of *Homo*, the likelihood of dependably describing sexual dimorphism and by extension mating behaviours in these species is poor. What is more, estimating the sex of specimens on the basis of *a priori*

notions of dimorphism introduces a degree of circularity as these sex estimations are then often used to make further statements about sexual dimorphism.

Sexual Dimorphism in Extant Primates

The use of analogs to model complex or unobservable processes is a common scientific practice. In the context of palaeoanthropology, the study of extant primates is essential to the development and refinement of paleontological theories through direct observation (Plavcan 2000). Compared to the human lineage, which is thought to be relatively derived, the branch that resulted in the great apes, is often assumed to be evolutionarily static – a retention of the primitive form (White *et al.* 2009). As a result, the hominin taxa near to the base of this branching point are thought to be comparatively more ape-like than human-like, creating the impression of morphological closeness with living apes, and lending credibility to their use as analogs. While allowing valuable insight into primate behaviour, direct comparison between living and extinct hominins is not without risk. Great ape evolution is even less well understood than human evolution, and though great apes are sometimes considered to be relatively unchanged from their last common ancestor with humans, research has demonstrated that a substantial degree of differentiation has occurred over the 5-8 million years of evolution that separate these taxa (Grehan 2006).

Although dental dimorphism is easier to study in extant species than fossil ones, it is still far from a perfect predictor of mating systems in living primates. Plavcan (2000) showed that not only were different dimorphic indicators non-uniformly capable of predicting systems of mating, but that in general, sexual dimorphism could only be moderately correlated with mating behaviour. Furthermore, it was discovered that while extreme dimorphism was strongly diagnostic of a polygynous system of mating, that the opposite was not true. Thus, species characterized by low levels of dimorphism were not, as a rule, monogamous or polyandrous. The generalization is even more weakly expressed in the dimorphic dentition of different species. Although body-size dimorphism is a strong predictor of polygyny and extreme competition among males, "modest or low degrees of canine-size dimorphism can be found among species with a wide variety of mating systems and competition levels" (Plavcan 2000: 341). The high levels of variance that were revealed in this study demonstrates the inability of current approaches to detect and account for the influence of alternate factors, exclusive of sexual selection, even in living forms, let alone fossil ones.

Conclusions

Hominin sexual dimorphism has been a focus of paleoanthropological study for nearly half a century, and though the strength of some morphology-behaviour correlates have been criticized (Begun 2004; Plavcan 2000, 2001, 2012; Plavcan *et al.* 2005; Rowell and Chism 1986), dental traits such as canine-size continue to serve as proxies for mating systems. On the basis of the extensive posterior tooth-size/body-size dimorphism detected in a number of species of *Australopithecus* and early *Homo,* it is theorized that these genera practiced some form of polygyny, characterized by intense intrasexual competition between males for access to mates. The low expression of canine-size dimorphism in these species alternatively indicates low competition levels and possibly a form of monogamy. This unique dental pattern has yet to be fully explained and shows only weak correlation with the mating systems of living primates.

Understanding the relationship between sexual dimorphism and mating behaviour in these genera is critical to comprehending how the dimorphic morphology of modern humans originated. Nevertheless, consistent problems have impaired attempts to reconstruct it. For one, many sources of variation are not well understood for their contribution to sexual dimorphism. Persistent difficulties detecting these additional factors in the fossil record means that these sources of variation often go unaccounted for. Although numerous different aspects of the dentition are dimorphic there is little agreement over the relative diagnostic value of each for indicating mating systems. What is more, because these different dimorphic characters are known to be the products of different selective processes they tend to produce ambiguous and potentially contrasting signals, the reasons for which are not always apparent. An important prerequisite for studying sexual dimorphism is the reliable differentiation of male and female morphology. Sex estimation in early hominins, however, is rarely certain; particularly when it is still unclear as to how some specimens should be classified taxonomically. Lastly, even in extant species, recent scholarship shows that dental dimorphism exhibits only moderate to weak correspondence with mating behaviour.

More generally, the field of palaeoanthropology is persistently troubled by low sample sizes and fragmentary specimens, few of which are spatially and temporally relatable, and a generally poor grasp of individual variation and taxonomic relationships. An improved knowledge of hominin sexual dimorphism, as always, could be improved by more fossil hominins of identifiable sexes, from within a unified context. It is also crucial to comprehend how alternate sources of variation such as diet, substrate preference, female competition, heritable processes, and sex roles impact the development of dental dimorphism. By better accounting for these processes it will become more feasible to detect and interpret the differences produced by conflict intensity and mating behaviour. Of equal importance, separate dimorphic characters must be evaluated and recognized as the products of different selective environments and their respective potential to indicate mating behaviour evaluated.

References Cited

Antón, Susan C., and Josh J. Snodgrass. 2012. Origins and Evolution of Genus *Homo*. *Current Anthropology* 53(6):479-496.

Begun, David. 2004. The three "Cs" of behavioural reconstruction in fossil primates. *Journal of Human Evolution 46*(4):497–505.

Berge, Christine, and Dionysis Goularas. 2010. A new reconstruction of Sts 14 pelvis (*Australopithecus africanus*) from computed tomography and three-dimensional modeling techniques. *Journal of human evolution* 58(3):262-272.

Berger, Lee R. 2012. *Australopithecus sediba* and the earliest origins of the genus *Homo*. *Journal of Anthropological Sciences* 90:1-16.

Bobe, Rene, and Anne K. Behrensmeyer. 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207(3):399-420.

Conroy, G. C. 2005. *Reconstructing Human Origins*. New York: W.W. Norton & Company, Inc.

Gingerich, Philip D. 1977. Correlation of tooth size and body size in living hominoid primates, with a note on relative brain size in *Aegyptopithecus* and *Proconsul*. *American Journal of Physical Anthropology* 47(3):395-398.

Gingerich, Philip D., B. Holly Smith, and Karen Rosenberg. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *American Journal of Physical Anthropology* 58(1):81-100.

Gordon, Adam D., David J. Green, and Brian G. Richmond. 2008. Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. *American Journal of Physical Anthropology* 135(3):311-328.

Grine, Frederick E., Gerhard W. Weber, J. Michael Plavcan, and Stefano Benazzi. 2012. Sex at Sterkfontein: 'Mrs. Ples' is still an adult female. *Journal of Human Evolution* 62(5):593-604.

Grehan, John R. 2006. Mona Lisa smile: the morphological enigma of human and great ape evolution. *The Anatomical Record Part B: The New Anatomist* 289(4):139-157.

Gruter, Margaret. 1982. Biologically based behavioural research and the facts of law. *Journal of Social and Biological Structures* 5(4):315-323.

Hager L. D. 1990. Was Lucy a female? *American Journal of Physical Anthropology* 81(2):234-234.

Harvey, Paul H., Michael Kavanagh, and T. H. Clutton-Brock. 1978. Sexual dimorphism in primate teeth. *Journal of Zoology* 186(4):475-485.

Häusler, Martin, and Peter Schmid. 1995. Comparison of the pelves of Sts 14 and AL288-1: implications for birth and sexual dimorphism in australopithecines. *Journal of Human Evolution* 29(4):363-383.

———. 1997. Assessing the pelvis of AL 288-1: a reply to Wood and Quinney. *Journal of Human Evolution* 32(1):99-102.

Hillson, Simon 1986. *Teeth*. England: Cambridge University Press.

———. 1996. *Dental Anthropology*. England: Cambridge University Press.

Lockwood, Charles A., Brian G. Richmond, William L. Jungers, and William H. Kimbel. 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. *Journal of Human Evolution* 31:537-548.

Kay, R. F., J. M. Plavcan, K. E. Glander, and P. C. Wright. 1988. Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology* 77(3): 385-397.

Lande, Russell 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34(2):292-305.

Lovejoy, C. Owen 2009. Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326(5949):74-74e8.

Lee, S. H. 2005. Patterns of size sexual dimorphism in *Australopithecus afarensis*: Another look. *Journal of Comparative Human Biology* 56(3):219-232.

Leutenegger, Walter, and James T. Kelly. 1977. Relationship of sexual dimorphism in canine size and body size to social, behavioural, and ecological correlates in anthropoid primates. *Primates* 18(1):117-136.

McHenry, Henry M. 1992a. Body size and proportions in early hominids. *American journal of Physical Anthropology* 87(1):407-31.

———. 1994a. Behavioural ecological implications of early hominid body size. *Journal of Human Evolution* 27(1/2/3):77-87.

McHenry, Henry M., and Katherine Coffing. 2000. *Australopithecus* to *Homo*: transformations in body and mind. *Annual review of Anthropology* 29:125-146.

Miller, Joseph 2000. Craniofacial variation in *Homo habilis*: an analysis of the evidence for multiple species. *American Journal of Physical Anthropology* 112(1):103-128.

Plavcan, J. Michael 2000. Inferring social behaviour from sexual dimorphism in the fossil record. *Journal of Human Evolution* 39(3):327-344.

———. 2001. Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology* 116(33):25-53.

———. 2004. Sexual selection, measures of sexual selection, and sexual dimorphism in primates. In *Sexual selection in primates: New and comparative Perspectives*. P. M. Kappeler and C. P. van Schaik eds. Pp. 230–252. Cambridge: Cambridge University Press

———. 2012a. Body Size, Size Variation, and Sexual Size Dimorphism in Early *Homo*. *Current Anthropology* 53(6):409-423.

———. 2012b. Sexual Size Dimorphism, Canine Dimorphism, and Male-Male Competition in Primates. *Human Nature* 23(1):45-67.

Plavcan, J. Michael, Charles A. Lockwood, William H. Kimbel, Michael R. Lague, and Elizabeth H. Harmon. 2005. Sexual dimorphism in *Australopithecus afarensis* revisited: How strong is the case for a human-like pattern of dimorphism?. *Journal of Human Evolution* 48(3):313-320.

Plavcan, J. Michael and Carel P. van Schaik. 1997a. Interpreting hominid behavior on the basis of sexual dimorphism. *Journal of human evolution* 32(4):345-374.

Plavcan, J. Michael, Carel P. van Schaik, and Peter M. Kappeler. 1995.
Competition, coalitions and canine size in primates. *Journal of human evolution* 28(3):245-276.

Reno, Philip L., Richard S. Meindl, Melanie A. McCollum, and C. Owen
Lovejoy. 2003. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proceedings of the National*

Academy of Sciences 100(16):9404-9409.

———. 2005. The case is unchanged and remains robust: *Australopithecus afarensis* exhibits only moderate skeletal dimorphism. A reply to Plavcan *et al.* (2005). *Journal of Human Evolution* 49(2):279-288.

———. 2010. An enlarged postcranial sample confirms *Australopithecus afarensis* dimorphism was similar to modern humans. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1556):3355-3363.

Rowell, T. E., and J. Chism. 1986. Sexual dimorphism and mating systems: jumping to conclusions. *Human Evolution* 1(3):215-219.

Shine, Richard. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64(4):419-461.

Sperber, G. 2013, January. Introduction to Odontology. *Anthropology: 584 – Advanced topics in Archaeology or Biological Anthropology.* Conducted at The University of Alberta, Edmonton, AB.

Spoor, F., M. G. Leakey, P. N. Gathogo, F. H. Brown, S. C. Antón, I. McDougall, C. Kiarie, F. K. Manthi, and L. N. Leakey. 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448(7154):688-691.

Strier, Karen B. 2007. *Primate Behavioural Ecology* (3rd ed.). United States of America: Pearson Allyn and Bacon.

Stringer, Chris and Peter Andrews. 2005. *The Complete World of Human Evolution*. London and New York: Thames and Hudson

Susman, Randall L. 2008. Brief communication: evidence bearing on the status of *Homo habilis* at Olduvai Gorge. *American Journal of Physical Anthropology* 137(3):356-361.

Tague, Robert G., and C. Owen Lovejoy. 1998. AL 288-1—Lucy or Lucifer: gender confusion in the Pliocene. *Journal of Human Evolution* 35(1):75-94.

Toth, Nicholas, and Kathy Schick. 2009. The Oldowan: The Tool Making of Early Hominids and Chimpanzees Compared. *Annual Review of Anthropology* 38:289-305.

White, Tim D., Berhane Asfaw, Yonas Beyene, Yohannes Haile-Selassie, C. Owen Lovejoy, Gen Suwa, and Giday WoldeGabriel. 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*, *326*(5949), 64-86.

Wilson, Edward O. 1975. *Sociobiology* (Abridged ed.). United States of America: Harvard University Press.

Wood, Bernard A. 1979. An Analysis of Tooth and Body Size Relationships in Five Primate Taxa. *Folia Primatol* 1:187-211.

———. 1996. Origin and evolution of the genus *Homo*. In *Contemporary issues in human evolution*. W. E. Meikle, C. F. Howell, and N. Jablonski eds. Pp. 105-114. San Francisco: California Academy of Sciences.

Wood, B. A., Y. Li, and C. Willoughby. 1991. Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. *Journal of anatomy* 174:185-205.

Wood, Bernard A., and Patrick S. Quinney. 1996. Assessing the pelvis of AL 288-1. *Journal of Human Evolution* 31(6):563-568.

Wolpoff, Milford H. 1976. Some Aspects of the Evolution of Early Hominid Sexual Dimorphism. *Current Anthropology* 17(4):579-606.